



PART 3

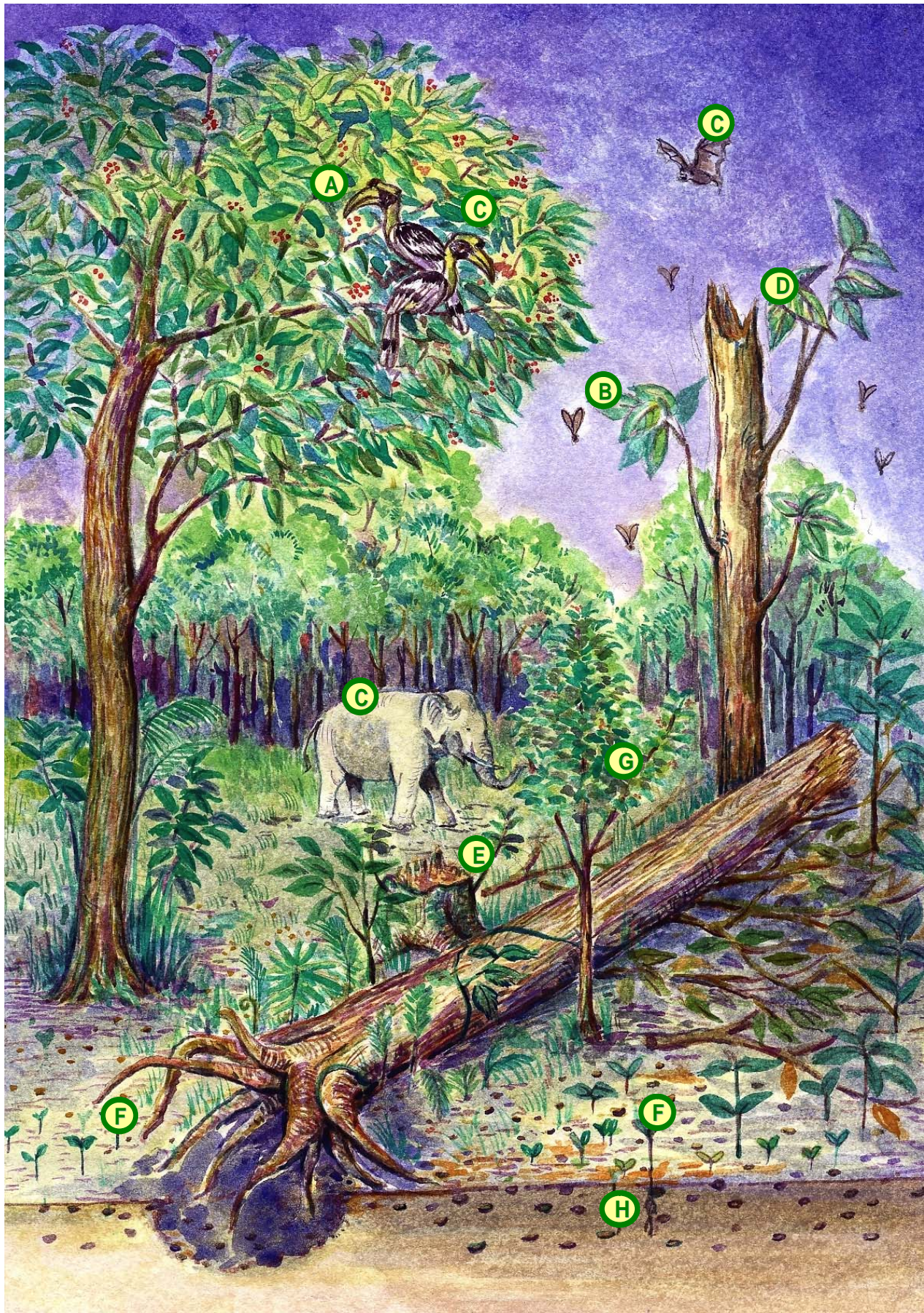
**UNDERSTANDING FOREST REGENERATION –
LEARNING FROM NATURE**

**THE THEORY OF FOREST SUCCESSION
SOURCES OF REGENERATION
THE IMPORTANCE OF SEED DISPERSAL
SEED PREDATION
GERMINATION
SEEDLING ESTABLISHMENT
THE ECOLOGY OF FIRE
THE SURVIVORS**

*“One of the penalties of an ecological education
is that one lives in a world of wounds”*

- Aldo Leopold

MECHANISMS OF FOREST REGENERATION



In tree-fall gaps within intact forest, succession proceeds rapidly. Nearby fruiting trees (A) provide a dense seed rain (B). Surrounding forest provides habitat for seed-dispersing animals (C). Damaged trees (D) and tree stumps (E) regrow. Seedlings (F) and saplings (G), formerly suppressed by the dense forest canopy now grow rapidly. Seeds in the soil seed bank germinate (H). In large deforested areas, created by humans, most of these natural mechanisms of forest regeneration are disabled.

UNDERSTANDING FOREST REGENERATION – LEARNING FROM NATURE

Some people take the view that deforested areas should be left to recover naturally and that forest restoration is unnecessary interference with nature. This view fails to recognize that the situation in most large deforested areas is far from “natural”.

Humans have not merely destroyed forest; we have also destroyed the natural mechanisms of forest regeneration.

The elimination of most large seed-dispersing animals by hunting now makes it almost impossible for climax forest to re-establish itself by natural means. Nearly all wildfires, which burn any tree seedlings that may become established, are also started by humans. Unless a concerted effort is made to restore the former mechanisms of forest regeneration, most deforested areas in the tropics will remain dominated by herbaceous weeds and maintained by frequent fires. Forest restoration is merely an attempt to correct the “unnatural” creation of so many large deforested areas by Humankind. Its success depends on a thorough understanding of the natural mechanisms of forest regeneration and consequently, development of methods to re-instate them (see Parts 4 & 5). Therefore, in this part, we present an overview of natural regeneration of seasonally dry tropical forest ecosystems, based mostly on FORRU’s research on the forests of Doi Suthep-Pui National Park in northern Thailand.

SECTION 1 - THE THEORY OF FOREST SUCCESSION

Ecologists regard forest regeneration as one particular example of “succession” – a series of predictable changes in ecosystem structure and composition over time, which if allowed to run its course, eventually results in a final, stable ecosystem, called the “climax” ecosystem. The climax ecosystem, for any particular area, depends on soil type and climatic conditions.

In Southeast Asia, wherever annual rainfall exceeds 1,000 mm, the climax ecosystem is some type of primary forest. Disturbance of primary forest, by tree cutting, fire and so on, causes it to revert to an earlier, temporary ecosystem in the successional series known as a “seral stage”. Once disturbance ceases, sequential changes in species composition occur due to interactions among plants and animals with their surrounding environment. Shrubs shade out grasses; trees shade out shrubs and light-demanding, pioneer tree species are eventually shaded out by shade-tolerant climax ones.

Thus, degraded grassland reverts back into forest, which becomes progressively denser, more structurally complex and more species-rich, as the processes of succession propel it towards the climax condition.

What are the differences between pioneer and climax tree species?

Tree species may be divided into two categories, depending on when they appear in the sequence of forest succession. Pioneer tree species are those that first colonize deforested sites. Over many years, as succession proceeds, they are gradually replaced by tree species characteristic of mature forest; the so-called climax tree species.

The main distinctions between pioneer and climax trees are that the seeds of pioneers can germinate only in full sunlight and their seedlings cannot grow in the shade that is cast by a forest canopy, whereas climax tree seeds can germinate in shade and their seedlings are shade tolerant.

Pioneer trees grow rapidly and usually produce large numbers of small fruits and seeds dispersed by the wind or small birds, at a young age. Pioneer tree seeds are easily dispersed over long distances and can lie dormant in the soil, before germinating when a gap is formed and light intensity increases. However, once the forest canopy closes, no more seedlings of pioneer species can grow to maturity.



Climax tree species grow for many years, consolidating their position in the forest ecosystem, before flowering and fruiting. They tend to produce large, animal-dispersed, non-dormant seeds, containing large food reserves, which sustain seedlings, whilst they grow slowly in shaded conditions. Therefore, climax tree species can regenerate beneath their own shade. This gives rise to the relatively stable species composition of climax forest.

In reality, these distinctions between pioneer and climax tree species are not so sharply defined. Some tree species may combine both pioneer and climax traits. For example, *Shima wallichii* (Theaceae) is an evergreen tree with small wind-dispersed seeds. This species readily colonises abandoned agricultural fields at elevations of 950-1,400 m, yet it is commonly found growing to a very large size in undisturbed evergreen forest. Furthermore, many climax tree species can perform as well as pioneers when planted out in deforested sites. Such tree species are not limited by the dry, hot, sunny conditions of deforested sites, but by lack of seed dispersal, since they tend to have large, animal-dispersed seeds.

This means that tree planting programs need not be restricted to pioneer species. Carefully selected, climax tree species can be planted simultaneously with pioneers to short-circuit succession and recreate a primary forest faster than would happen naturally. So, succession can be manipulated both forwards and backwards. Tree cutting reverses it, whilst forest restoration activities accelerate it forwards.

So why don't forests grow back naturally?

If nature has such remarkable powers of self-regeneration, why is forest restoration necessary? When a dead tree falls to the ground in a forest, a hole is created in the forest canopy. For the first time in decades, the forest floor is bathed in sunlight, which stimulates an intense struggle amongst a surplus of existing tree seedlings and saplings to grow and fill the gap. Only the fastest-growing tree will win. All the others will fade away in the victor's shade. Within a few years, the tree that died will be consumed by termites and fungi, releasing its nutrients into the soil. In its place, another tree








will stand, perhaps for a hundred years or more until one day, a violent storm may send it crashing to the ground, to be recycled like its predecessor.

Within small gaps in tropical forest, natural processes of self-regeneration work efficiently to bring about swift forest recovery. In contrast, in large deforested areas, forest regeneration is either very slow or fails to occur at all.

Large deforested areas can be caused by natural catastrophes, such as volcanic eruptions or cyclones, but such occurrences are rare. Today, wide-spread deforestation is mostly the result of human activities such as logging, slash-and-burn agriculture and infrastructure development. Where disturbances are frequent, natural succession is impeded, resulting in a persistent pre-climax ecosystem (termed "plagio-climax"). Under such circumstances, natural mechanisms of succession are insufficient to restore the original forest ecosystem. The cycle of degradation must be broken by counteracting the factors that prevent tree establishment and, where a seed supply is limiting, by tree planting.

What factors limit forest regeneration in large deforested areas?

In the large, open, deforested areas, that remain after logging or cultivation, the establishment of forest trees depends on seeds being dispersed into the areas. The seeds must land where conditions are suitable for their germination and they must escape the attention of seed-eating animals - the so called "seed predators". After germination, tree seedlings must win an intense competition with weeds for light, moisture and nutrients. The growing trees must avoid being burnt by wildfires or eaten by cattle. The factors that limit forest regeneration are therefore:-

-  Lack of a seed source
-  Lack of seed dispersers
-  Seed predation
-  Unsuitable soil and microclimatic conditions for germination and early seedling growth
-  Dominance by herbaceous weeds
-  Fire
-  Browsing by domestic animals



SECTION 2 – SOURCES OF REGENERATION

All trees start life as seeds, so forest succession ultimately depends on the presence of fruiting trees nearby. In a largely deforested landscape, some tree species may be represented by a few scattered, isolated, individuals that somehow escaped the axe or chain saw, or there may be remnant forest patches producing seeds of a wider range of tree species. Distances from seed sources have a critical effect on the rate of forest regeneration and on the diversity of the tree species that grow back in any particular location. Fruiting trees not only provide seeds for forest regeneration, they also attract frugivorous, seed-dispersing animals. Therefore, protection of any fruiting trees in a deforested landscape will greatly enhance natural forest regeneration.

When do forest trees produce seed?

In a tropical forest, fruiting is highly variable among species, among sites and from year to year. Most tree species fruit once per year, but some fruit twice per year and a few, such as the talipot palm (*Corypha umbraculifera*) have one big fruiting event just before dying (a fruiting pattern termed “monocarp”). Another fruiting pattern, common amongst tree species of the Fagaceae (oaks and chestnuts) and Dipterocarpaceae is known as “masting”, when an entire species population fruits heavily and synchronously at intervals of several years.

Different tree species flower and fruit at different times of the year, but at the community level, seasonal cycles in fruiting and seed dispersal are evident, particularly in seasonally dry tropical

forests. The study of these seasonal cycles is called forest phenology.

In Doi Suthep-Pui National Park, tree species with wind-dispersed seeds tend to develop their fruits and seeds during the dry season. Very few wind-dispersed tree species fruit in the rainy season. Tree seed dispersal by wind peaks at the end of the dry season in April, when 43% of wind-dispersed tree species release their seeds. Not surprisingly, this is also when the strongest winds occur during pre-monsoon storms (Elliott *et al.*, 1994). In contrast, the number of animal-dispersed tree species in fruit is fairly high all year round, but gradually increases during the rainy season, peaking towards the end of the rainy season in September (when 37% of animal-dispersed tree species bear fruit) (see Fig 3.1).

Figure 3.1 - Seasonal cycles of fruiting in animal-dispersed (283 species) and wind-dispersed (136 species) tree species, Doi Suthep-Pui National Park, northern Thailand (source: CMU Herbarium Database , J. F. Maxwell)

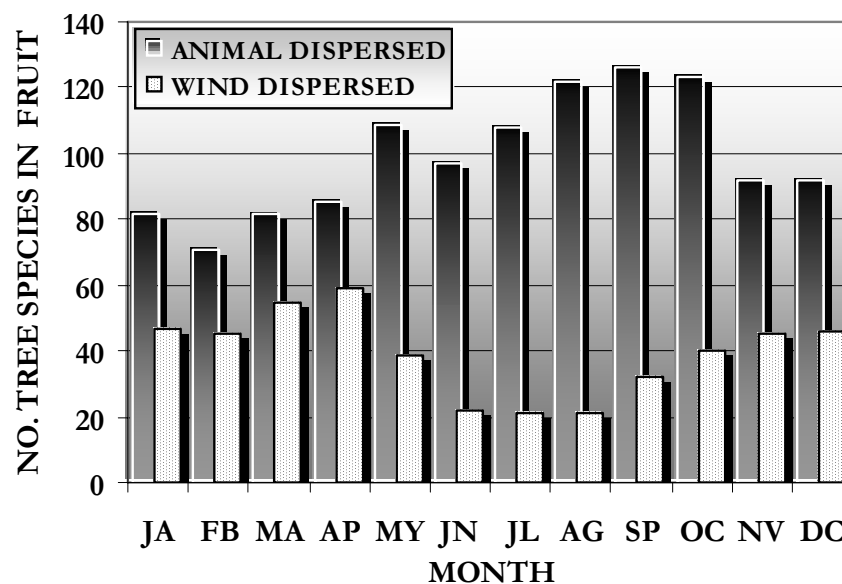
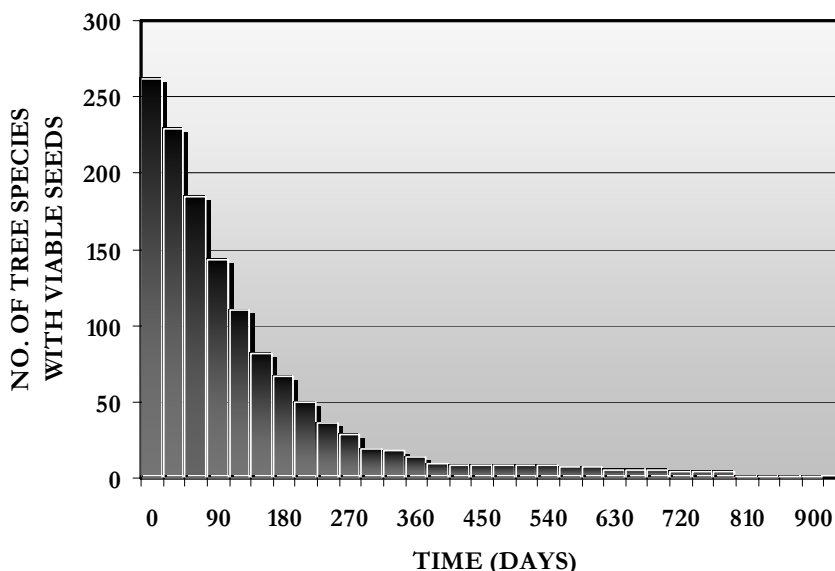


Figure 3.2 - After deforestation, the number of original forest tree species represented by viable seeds in the soil seed bank declines exponentially over time (data from FORRU's nursery experiments).



What is the soil seed bank?

The soil seed bank is the number of viable seeds present in a known volume of soil. It is usually measured by taking core-samples of soil (often sub-divided by depth), spreading the soil in germination trays, watering it and then counting the numbers of seeds that subsequently germinate. It is usually expressed as numbers of seeds per cubic metre of soil. For studies of forest regeneration, the soil seed bank can be divided into those seeds remaining from the original forest and those that have been dispersed into the area since deforestation occurred.

Where deforestation has been followed by prolonged or repeated disturbances, it is unlikely that seeds from the original forest play a major role in forest regeneration. Although a few tree species produce seeds that can survive dormant in the soil for 2-3 years, seeds of the vast majority of tropical tree species lose their viability within a few weeks or a few months after dispersal has occurred.

Of 262 tree seed species from northern Thailand, which were tested in FORRU's research nursery, only 5.3 percent produced seeds with a maximum dormancy of longer than a year (see Fig. 3.2, above).

Therefore, in most deforested sites older than a few years, the soil seed bank is comprised of seeds dispersed into the area from nearby fruiting trees. Efficient dispersal of seeds from trees in nearby forest into deforested areas is therefore of paramount importance for natural forest regeneration to occur.

Are there other sources of forest regeneration besides seeds?

Some tree species can re-grow from old tree stumps or root fragments, years after the original tree was chopped down (Hardwick *et al.*, 2000). Dormant buds around the root collar of a tree stump can spontaneously sprout, often generating several new shoots. This is called coppicing. Both climax and pioneer tree species can re-grow in this way (de Rouw, 1993). Coppicing stumps have greater resilience to fire and browsing than seedlings. Drawing on food reserves stored in the roots, they can rapidly grow above surrounding weeds. Consequently, such regeneration can greatly accelerate re-establishment of tree cover. Protecting tree stumps, therefore, gives forest regeneration a head start, whereas destroying them delays it.

There is much variation among tree species in their ability to coppice and there is no adequate model to predict which species can coppice and which cannot. Larger stumps tend to produce more vigorous shoots, in greater numbers, than smaller stumps. Furthermore, taller stumps survive fire, browsing and weed competition better than shorter ones, since the shoots are usually above the height of disturbance.

In any deforested site, tree species regenerating from stumps represent a small proportion of the total original tree community of the former forest ecosystem. Although such trees can accelerate recovery of forest structure, seed dispersal is still essential to restore the tree species richness of the original forest.



SECTION 3 – THE IMPORTANCE OF SEED DISPERSAL

What is the seed rain?

The seed rain consists of all seeds falling on to any particular area of land. It is often measured using seed traps, to capture seeds falling on to small, sample plots, of known area, and is expressed in terms of numbers of seeds, per metre squared, per month, often subdivided by plant species, plant habit (tree, herb and so on) or dispersal mechanism. The density and species composition of the seed rain, on any deforested site, depends on the nearness of fruiting trees and on the efficiency of dispersal mechanisms. The seed rain is most dense and contains more tree species near to intact forest and is sparse in the centre of large deforested areas.

Most tree seedlings, establishing on large, deforested sites, germinate from seed either blown on to such sites by the wind or carried there by birds, bats or other animals. A depleted seed rain is one of the major causes of lack of forest regeneration or low species richness among the tree communities colonizing such sites. Encouraging seed dispersal is therefore a vital element of forest restoration.

How important is wind-dispersal of seeds?

In the forests of northern Thailand, dispersal of tree seeds by animals is more common than by wind. Of the 475 tree species recorded for Doi Suthep-Pui National Park, only 29% are wind-dispersed. In deciduous dipterocarp-oak forest, 44% of tree species (approximately 62% of individual trees) rely on the wind for seed dispersal. In contrast, in evergreen forests, only 21% of tree species (approximately 11% of individual trees) are wind-dispersed.

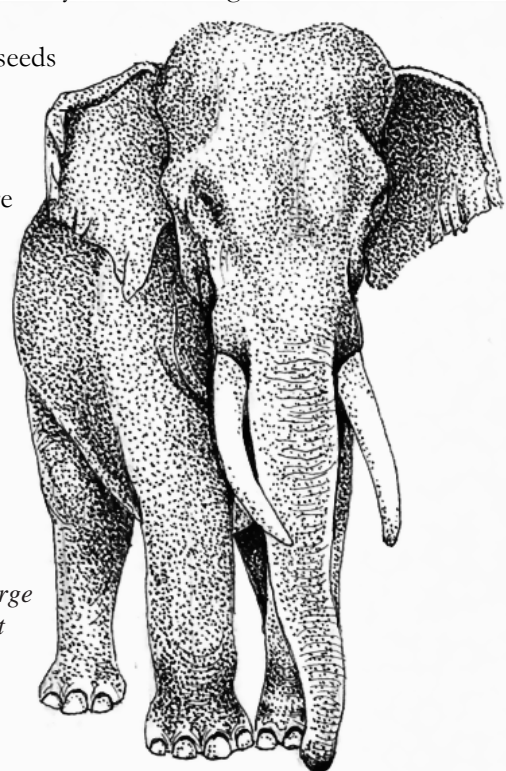
Wind-dispersed seeds tend to be small and light and often have wings, which slow their fall, enabling them to drift over considerable distances. Therefore, wind-dispersed tree species can usually colonize deforested sites fairly easily. If existing conditions allow such species to become naturally established, there is no need to include them in tree planting programs.

What animals are seed dispersers?

Most tree species depend on animals to disperse their seeds. Some seeds become attached to fur or feathers and are transported on the outside of animals' bodies (termed "ectozoochorous" dispersal). More commonly, fruits are eaten and the seeds discarded or swallowed (dispersed whilst in the gut) and defaecated far away from the parent tree (termed "endozoochorous dispersal"). Such fruits tend to be brightly coloured to attract animals, and fleshy, providing a reward of food to their animal dispersers.

Dispersal of seeds from forest into deforested sites, therefore, depends on animals that regularly move between the two habitats. Unfortunately, rather few forest animals venture out into open areas, for fear of exposing themselves to predators. Compared to wind, animals are rather inefficient seed dispersers. Apart from birds and bats, few animals travel very far between eating a fruit and defaecating the seed. Furthermore, many seeds are crushed by teeth or destroyed by digestive juices.

The maximum size of seeds dispersed by any animal species depends on the size of the animal's mouth. Whilst small animal species are still relatively common, larger ones, capable of swallowing large seeds whole, have been largely wiped out by hunting. Small seeds are therefore more easily dispersed into deforested areas by animals than larger ones.



Elephants can disperse very large seeds from forest into deforested areas.



In the past, large herbivores were undoubtedly the most important dispersers of seeds from forest into deforested areas. Elephants, rhinos and wild cattle often consume fruit in the forest, emerging into open areas at night to graze. With their large mouths and long roaming distances, such animals could swallow the largest of seeds and transport them over long distances. The elimination of most of these large mammals, over much of their former ranges in recent decades is now preventing dispersal of many tree species with very large seeds (Corlett and Hau, 2000).

Because they can fly, birds and bats can also disperse seeds over long distances. Amongst the birds, bulbuls are particularly important. They are common in forest and are frequent visitors to deforested sites, several kilometres from natural forest (Scott *et al.*, 2000). They disperse seeds of a very wide range of plant species (Sanitjan, 2001), up to 14 mm in diameter over long distances, since they retain seeds in their digestive tracts for up to 41 minutes (Whittaker and Jones, 1994). Other common bird species, which probably contribute to the seed rain of deforested areas, include mynahs, jays, magpies, thrushes, robins, chats, white-eyes, laughing thrushes and flowerpeckers (Corlett and Hau, 2000). Many of these are insectivores, which also take fruit as part of their diet. Near to intact forest, green pigeons, Oriental Pied Hornbill and, at higher elevations, wood pigeons probably play a role in seed-dispersal.

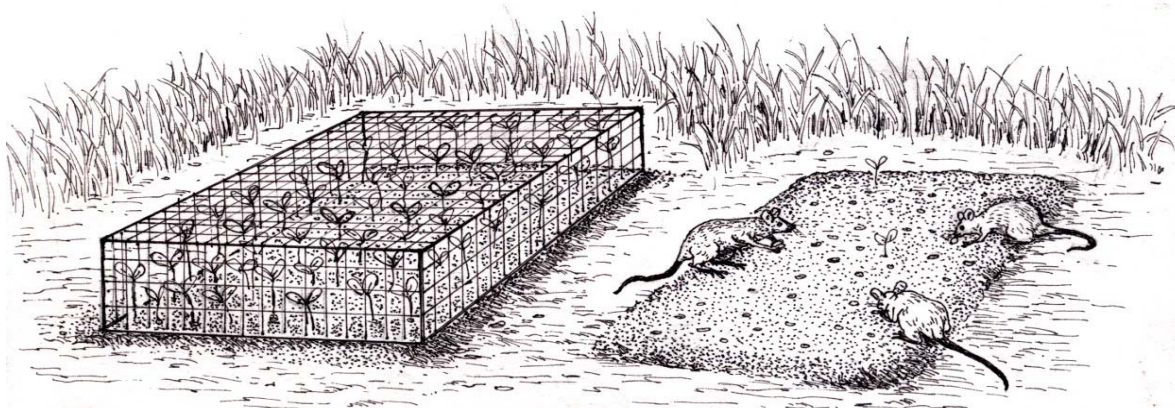
Fruit bats are important seed dispersers, since they fly over long distances and drop seeds in flight. However, unlike most birds, bats are nocturnal and cannot be identified using binoculars. Consequently, little research has been done on their role in forest regeneration. Research on bats is, therefore, a high priority for improvement of forest restoration techniques¹.

Non-flying mammal species that remain common and are likely to disperse seeds between forest and degraded areas include Common Wild Pig, Common Barking Deer, Hog Badger and various civet species, but again, largely due to their nocturnal habits, very little information is available on the seed dispersing capabilities of these animals.

How far are seeds dispersed?

Most tree seeds fall within a few metres of the parent tree. The density of a single tree's "seed shadow" declines steeply with distance away from the tree. However, according to Clark (1998), approximately 10 percent of tree seeds are dispersed over much longer distances of 1 to 10 km. Little is known about this long-distance component of the seed rain, since it is very difficult to measure. However, it is an important consideration in the design of forest restoration projects, particularly with respect to the distance of forest restoration plots from intact forest and how this will affect recovery of tree species richness.

Rats are major seed predators in deforested areas in northern Thailand. Their impact on seed survival has been measured by caged exclusion experiments (Box 3.1).



¹The Chiang Mai Research Agenda for the Restoration of Degraded Forestlands for Wildlife Conservation in Southeast Asia, Part 7 of Elliott, S., J. Kerby, D. Blakesley, K. Hardwick, K. Woods and V. Anusarnsunthorn (eds.), *Forest Restoration for Wildlife Conservation*. Chiang Mai University (2000).



SECTION 4 - SEED PREDATION

If seeds deposited in deforested areas are to germinate, they must avoid being killed by animals. A single tree produces vast numbers of seeds during its lifetime, although, to replace itself, it need produce only one that eventually grows into a reproductively mature adult. The need for such excessive seed crops is because most seeds either fall where conditions are unfavorable for germination or they are destroyed by animals. Because many seeds contain rich reserves of oils and carbohydrates, they often end up becoming nutritious meals for animals. Whilst some seeds may pass through the digestive tracts of animals intact, many others are crushed by teeth and digested.

What is seed predation?

Seed predation is the destruction of a seed's potential to germinate when an animal crushes or digests its embryo. It can occur when seeds are attached to the parent tree (pre-dispersal predation). However, seed predators have more impact on forest regeneration when they attack seeds that have already been dispersed into deforested areas (post-dispersal predation).

What animals are seed predators in regenerating forest?

Small rodents and insects, particularly ants, are major seed predators. In deforested areas in northern Thailand, rats and mice such as *Mus pahari*, *M. cookie*, *Rattus bukit*, *R. koratensis*, *R. surifer* and *R. rattus* are the most prevalent rodent seed predators. These animals are more common in deforested sites than in forest (Sharp, 1995). If forest regeneration progresses to the point of canopy closure, rodent populations decline markedly (Thaiying, 2003). Therefore, tree planting reduces seed predation.

Ants have been recognised as major seed predators in Central and South America (Nepstad *et al.*, 1996), but their potential impact on forest regeneration in Asia is only just becoming apparent (Woods and Elliott, 2004). More research is needed on the seed-eating habits of ants in deforested areas in Asia.

What levels of seed predation can be expected in deforested areas?

In the tropics, more than 90% of tree species have more than 50% of their seeds killed by animals or fungi. Seed predation has a significant effect on both the distribution and abundance of tree species. It is also a potent evolutionary force, compelling trees to evolve various morphological and chemical mechanisms to defend their seeds against animal attack *e.g.* poisons, tough seed coats and so on.

Levels of seed predation are highly unpredictable, varying from 0 to 100 percent, depending on tree species, vegetation, location, season and so on. In general, however, seed predation in deforested areas is usually severe enough to significantly reduce seed survival of most tree species (see Box 3.1 & Hau, 1999).

What determines the susceptibility of seeds to predation?

Ecological theory suggests that the susceptibility of any particular tree species to seed predation depends on the food value of its seed. Animals should consume seeds that provide them with maximum nutriment, whilst requiring the least effort to find them.

Most attention has been paid to the influence of seed size on vulnerability to predation. Large seeds provide large food rewards to those seed predators that are capable of processing them. Animals may be able to locate large seeds easily, since they are more visible and emit more odour than small seeds, but small rodents have difficulty handling very large seeds. In contrast, small seeds have low food value and are easily overlooked. Vongkamjan (2003) confirmed this effect of size on tree seed predation in evergreen forest clearings in northern Thailand. She observed seed predation rates of zero for all tree species tested which had small seeds (seeds weighing less than 0.01 gm); 50-91 percent for 4 of 10 medium-sized seed species (0.01 – 0.2 gm; the others had removal rates of less than 1%) and 63-100% for 6 of 10 large-seeded species (0.2 – 6.2 gm; four others had removal rates of less than 2%).





Box 3.1 - Forest Tree Seed Predation in Northern Thailand

The effects of seed predation by rodents can be measured by placing seeds inside wire-mesh cages, to exclude rodents. Germination of seeds inside the cages is then compared with that of seeds placed outside cages nearby and exposed to predation.

Using this technique in a medium-sized clearing (about 50 m across), surrounded by evergreen forest in Doi Suthep-Pui National Park, Hardwick (1999) found that the mean germination percentages of 8 out of 12 tree seed species, exposed to predation were reduced by 50% or more, compared with seeds protected within cages (*i.e.* *Castanopsis acuminatissima*, *Engelhardia spicata*, *Eurya acuminata*, *Helicia nilagirica*, *Hovenia dulcis*, *Prunus cerasoides*, *Schima wallichii* and *Styrax benzoides*). Only the tiny seeds of *Morus macroura* escaped significant predation, perhaps because rodents are unable to find them.

Similarly, in small tree-fall gaps nearby, Vongkamjan (2003) recorded seed predation

rates of 100% for *Irvingia malayana* and *Elaeocarpus prunifolius*, 91% for *Reevesia pubescens*, 88% for *Terminalia chebula*, 77% for *Shorea obtusa*, 73% for *Terminalia mucronata*, 69% for *Terminalia bellirica*, 65% for *Macropanax dispermus*, 63% for *Elaeocarpus lanceifolius* and 50% for *Acrocarpus fraxinifolius*. Again, tree species with zero seed predation were those with tiny or medium-sized seeds *e.g.* all *Ficus* spp, *Morus macroura*, *Betula alnoides*, *Debregeasia longifolia*, *Saurauia roxburghii*, *Eurya acuminata*, *Vaccinium sprengelii*, *Trema orientalis*, *Tetradium glabrifolium*, *Lagerstroemia speciosa* etc.

In contrast, in a much larger area of abandoned agricultural land at a similar elevation on the same mountain, Woods and Elliott (2004) found no significant seed predation of six tree species (*i.e.* *Sapindus rarak*, *Lithocarpus elegans*, *Spondias axillaris*, *Erythrina subumbrans*, *Gmelina arborea* and *Prunus cerasoides*) by rodents, although predation by ants was high on the latter four species.

The longer a seed lies on the ground before germinating, the higher is the probability that a predator will discover it. Rapid germination reduces the period during which seed predation can occur. Hardwick (1999) reported a positive relationship between length of seed dormancy and seed predation rates in evergreen forest clearings in northern Thailand.

The nature of the seed coat is important in protecting seeds from predation. A tough, thick and smooth seed coat makes it very difficult for rodents to reach the nutritious seed contents. Low predation rates amongst seeds with thick or hard seed coats have been reported for many Asian forest tree species (*e.g.* Hau, 1999; Vongkamjan, 2003). However, there may be a trade-off between seed coat thickness and length of dormancy in their effects on seed predation. A thick seed coat often causes prolonged dormancy, which lengthens the period during which seeds are available for attack by predators. But, even the toughest seed coat must soften, just before germination, presenting a window of opportunity for seed predators. Vongkamjan (2003) observed that several hard-coated tree seed species were attacked during this vulnerable period.

Dispersal pattern may also affect likelihood of predation. Seeds that are scattered thinly over a large area (a pattern that often results from wind-dispersal) are hard to find by predators, whereas a clumped dispersal pattern (characteristic of animal-dispersal) means that once one seed has been discovered, the whole clump will probably be predated. Sporadic large fruit crops, such as those produced by masting or monocarpy (Section 2, this part) satiate seed predator populations. Seed predators cannot possibly eat all the seeds, so many seeds escape predation.

Models capable of predicting the overall effects of seed predation on forest regeneration have proved elusive. The literature is full of contradictory statements and opposing viewpoints. The effects of seed predation undoubtedly depends on complex interactions among many variables, including the nature of the environment, availability of alternative food sources and the individual preferences and seed handling capabilities of the particular seed predator species present. It is certainly a factor that must be considered in forest restoration projects that involve direct seeding, but its effects must be evaluated for each individual site.



SEED DISPERSERS & SEED DESTROYERS



Small and medium-sized seed-dispersing animals, such as the Hog Badger,

(Arctonyx collaris) (below), Large Indian Civet (Viverra zibetha) (above) and Flavescent Bulbul (Pycnonotus flavescens) (right) can remain common even in highly fragmented forest landscapes. They can disperse seeds over long distances from forest into large deforested areas. Preventing hunting of them is a vital component of forest restoration projects.



The Chestnut Rat (Rattus bukit) (below) rarely disperses seeds, but usually destroys them. They are more common in deforested areas than in closed forest.



Other seed-dispersers, such as the White-Handed Gibbon (Hylobates lar) (above left) and the Indian Pied Hornbill (Anthracoceros albirostris) (above center) rarely leave dense forest and so are unlikely to contribute much to the seed rain of open, deforested areas.



Peter Schwendinger

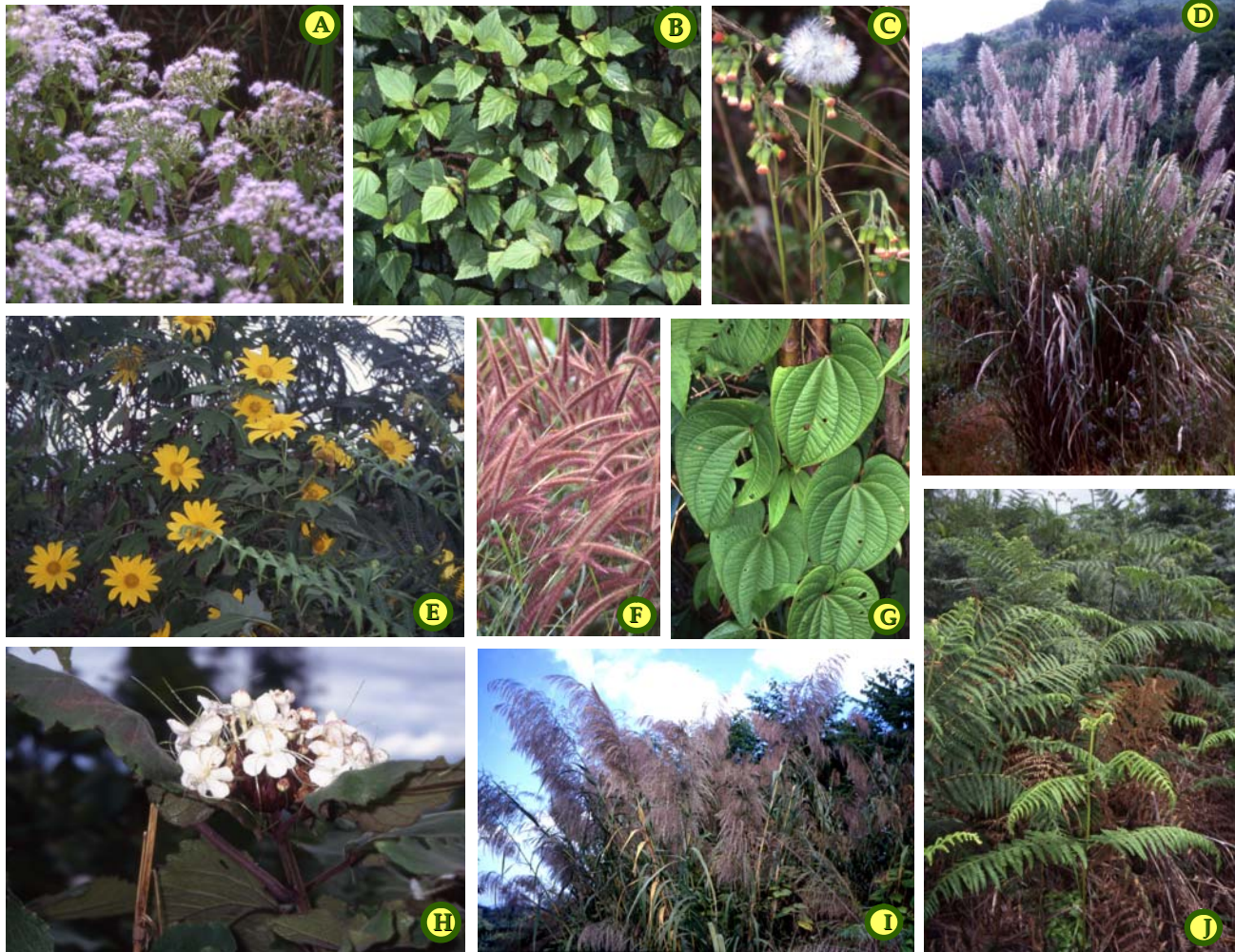
Often feeding on fallen fruits in the forest during the day time and emerging at night to browse in clearings, the Sumatran Rhino was the perfect seed disperser for forest regeneration. Now, sadly, this species has been extirpated from northern Thailand and several other large animals, such as elephants and wild cattle have been reduced to such low populations that they no longer play a significant role in seed dispersal.



THE COMPETITION



Deforested sites in northern Thailand are usually dominated by aggressive, fire-resilient grasses and herbs, which often grow above head-height (left). Many are exotic weeds, which are particularly successful at invading and persisting in degraded areas. These fast-growing plants prevent tree establishment by smothering tree seedlings; by absorbing most of the soil moisture and nutrients that would otherwise be available for tree growth and by providing fuel for fires.



*Common herbaceous weed species in degraded sites include several exotic species such as (A) *Eupatorium odoratum*, (B) *Eupatorium adenophorum*, (C) *Crassocephalum crepidioides* and (E) *Tithonia diversifolia* (Mexican Sunflower) as well as dominant native grasses such as (D) *Saccharum arundinaceum*, (F) *Pennisetum polystachyon* and (I) *Phragmites vallatoria*. Vines such as (G) *Dioscorea bulbifera* smother tree seedlings, whilst the shrub (H) *Clerodendrum fragrans* shades them from above. Bracken fern (J) *Pteridium aquilinum* is found all around the world.*



SECTION 5 – GERMINATION

The transition from seed to seedling is a dangerous time in a tree's life. Seed dormancy must end and appropriate levels of moisture and light must exist to trigger germination. Because of its small size, low energy reserves and low photosynthetic capability, a young seedling is very vulnerable to changes in environmental conditions, competition from other plants and attack by herbivores. A single caterpillar can completely destroy a young seedling in a few minutes, whereas larger plants are more resistant to attack.

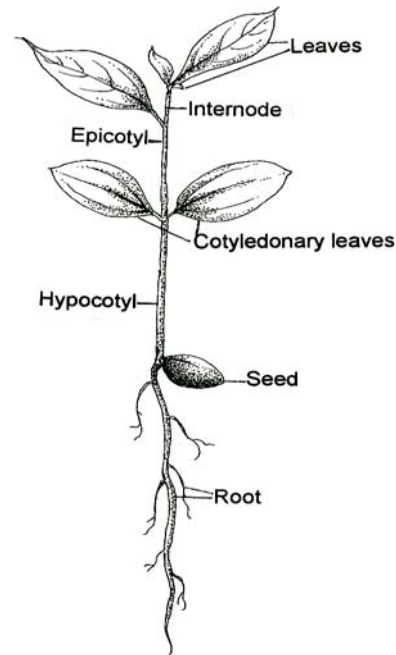
What is seed dormancy?

After being deposited in a deforested site, a seed might not germinate immediately, even where conditions for germination are optimal. Dormancy is the period between seed dispersal and germination. During dormancy, some seeds undergo maturation or chemical changes that prepare the seed for germination. Dormancy enables seeds to survive the rigours of dispersal and germinate when conditions are most favourable for seedling establishment.

How long do seeds lie dormant?

In any batch of seeds, the length of dormancy of individual seeds can be variable. The most convenient overall measure of dormancy is the number of days between seed sowing and germination of half the total seeds that eventually germinate. This is the "median length of dormancy" (MLD). For example, if 9 seeds eventually germinate out of 100 sown, MLD would be the number of days between seed sowing and germination of the 5th seed.

Seeds of most tropical tree species have short dormancy periods. In a sample of 262 forest tree species examined from Doi Suthep-Pui National Park, 43% had MLD's of less than 30 days, whilst only 21% had MLD's of more than 100 days. Tree species with the shortest MLD's were *Albizia odoratissima*, *Erythrina subumbrans* and *Quercus lanata* (all 7 days). *Elaeocarpus bracteanus* had the longest recorded MLD of 787 days (FORRU-CMU, original data, 2003).



When is the best time for seed germination?

Many factors determine the optimal period for germination (*e.g.* temperature, avoidance of seedling predators and so on). However, in the seasonally dry tropics, soil moisture appears to be the overriding factor. The optimal time for tree seed germination is the start of the rainy season. Seedlings establishing then have the full length of the rainy season to grow their roots deep into the soil and to build up energy reserves before onset of the dry season. A deep root system allows seedlings to tap into stored soil moisture that will enable them to survive the desiccating heat of their first dry season. Another reason for germination at the start of the rainy season is the release of nutrients from litter. Moisture encourages decomposition and, where they occur, fires also release nutrients.

Optimal seed dispersal time varies greatly among tree species. The length of time required to develop a mature fruit from a fertilised flower and the availability of dispersal agents are just two species-specific characteristics that determine optimal seed dispersal time. Different lengths of seed dormancy amongst different tree species allow tree species to disperse their seeds at different times throughout the year, whilst maintaining a peak in germination around the beginning of the rainy season. FORRU's research on this topic is presented in Box 3.2.





Box 3.2 – Seed dormancy links optimal dispersal time with optimal germination time.

Different forest tree species produce seeds at different times of the year, but different seed dormancy lengths, amongst the species, ensures that, whenever seeds are produced, most species germinate at the start of the rainy season.

A study of seed dispersal and germination of 262 tree species collected in the forests of Doi Suthep-Pui National Park, (FORRU-CMU, original data, 2003) found that most seeds collected in the late dry and early rainy seasons germinated rapidly (>90% had MLDs of <71 days). In contrast, for seeds collected in the late wet and early rainy seasons, only 48.5% and 54.8% of species, respectively, germinated rapidly (MLDs <71 days). The others remained dormant for long periods. Consequently, the median seed of 75.8% of species studied germinated in the late dry or early rainy seasons.

This timing allows maximum seedling development to occur before onset of the dry season and minimises the period that seeds lie dormant on the forest floor, consuming energy by respiration and at risk from seed predators.

Species could be grouped according to dispersal time and dormancy syndromes. The ‘rapid-rainy group’ was comprised of 171 species, which dispersed their seeds late in the dry season and during the rainy season. These species germinated rapidly in the rainy season. In contrast, the ‘delayed-rainy group’ was comprised of 62 species, which dispersed their seeds late in the rainy season and early in the dry season. They had prolonged dormancy, resulting in germination in the subsequent rainy season. Another distinct group, the ‘rapid-dry group’ had 34 species, which dispersed their seeds in the early dry season and germinated rapidly in the same season. The survival strategies of this latter group deserve further research.

A very similar pattern of seed dispersal and germination was observed in Panama by Nancy Garwood (1983), suggesting that seasonally dry tropical forests on at least two separate continents have evolved similar strategies to overcome the common constraints imposed by annual cycles of wet and dry.

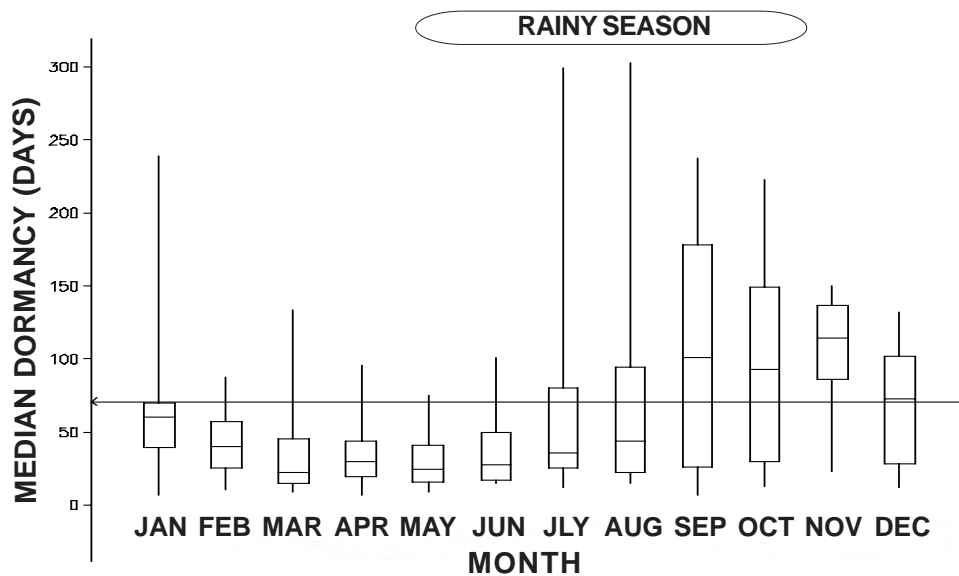


Figure 3.3 - The relationship between median length of dormancy (MLD) and the month of seed dispersal of forest tree species in Doi Suthep-Pui National Park. Each box represents 50 % of the number of tree species dispersed in each month. The horizontal line within each box indicates the median value of all MLDs, averaged across all species dispersed in each particular month, whilst extreme values are indicated by the thin vertical lines.



What conditions are required for seed germination?

Seed germination depends on many factors, the most important of which are sufficient soil moisture and light conditions, not only total light levels, but also the quality of the light.

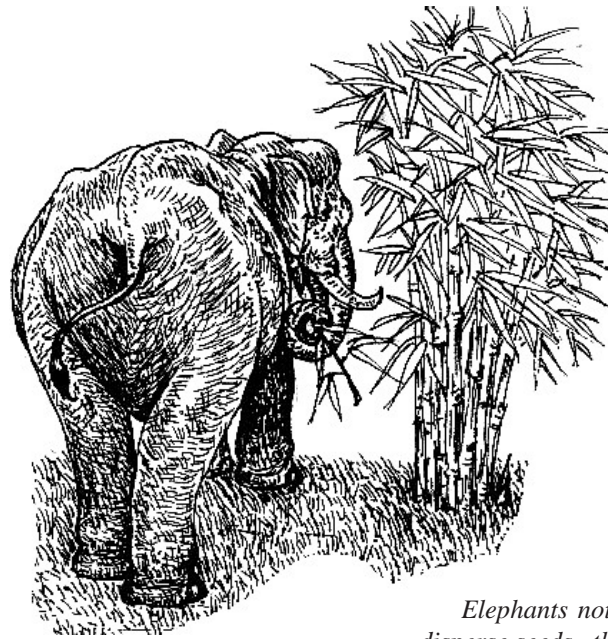
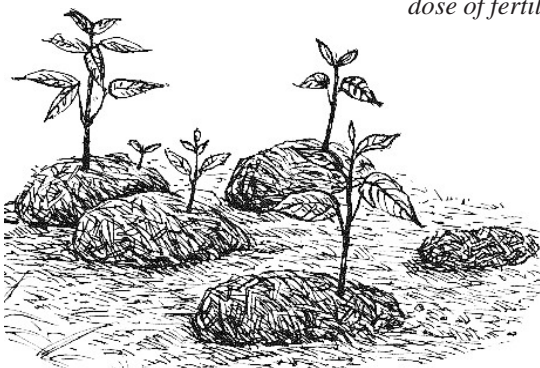
Within intact forest, the species of tree seedlings that establish in any small, tree-fall, gap depends initially on the species composition of the seed rain and subsequently on the micro-climatic conditions within the gap. The latter depend on the size, shape and aspect of the gap and the density and height of the trees that surround it. Which seed species fall into a gap depends on which tree species are seeding nearby and on the chance events that affect dispersal mechanisms. Subsequently, gap-dependent conditions selectively favour or eliminate the species present, according to the micro-climatic requirements of each species.

Large, deforested sites, dominated by dense weeds present a far more hostile environment to tree seeds. Temperatures fluctuate dramatically between night and day. Humidity is lower, wind speeds are higher and soil conditions are much harsher.

Many seeds become trapped in the weed canopy, where they dry out and die, never to reach the soil. Even for seeds that fall through the weed canopy, weeds present another problem. A high ratio of red to far red light in the spectrum stimulates seed germination in many pioneer tree species, particularly those with small seeds (Pearson *et al.*, 2003). By absorbing proportionately more red light than far red light, a dense green canopy of weed foliage removes this vital stimulus.

Therefore, seed germination of most forest tree species depends on the presence of

...and provide them with a generous dose of fertilizer.



Elephants not only disperse seeds, they may also enhance germination of some species...

so-called “germination micro-sites”, where conditions are more favourable. These are tiny sites with reduced weed cover and sufficient soil moisture to induce seed germination. They include decaying termite mounds, rocks covered in moss and especially rotting logs. The latter provide an excellent moist and nutrient-rich medium for seed germination and are usually weed free.

Do animals enhance germination?

Passage of seed through an animal’s gut can affect both total germination percentage and the rate of germination. These properties can be enhanced, inhibited or unaffected. For most tropical trees, passage through an animal has no overall effect on germination, but for those species showing a response, germination is enhanced more often than it is inhibited. Travaset (1998) reported that ingestion by animals increased germination percentage of 36% of tree species tested, whilst it reduced germination percentage for only 7%. Seeds of 35% of tree species tested germinated more rapidly after passage through an animal’s gut, compared with only 13% that had more delayed germination. Responses are highly variable. Seeds of species within the same genus, or even from different individual plants of the same species, can have different responses.



SECTION 6 – SEEDLING ESTABLISHMENT

After a seed has germinated, the greatest threats to seedling survival in deforested areas are fire and competition with weeds. Deforested areas are usually dominated by fire resilient, herbs and grasses. By absorbing most of the sunlight and draining the soil of moisture and nutrients, these rapidly growing weeds leave few resources for slower growing tree seedlings. However, tree seedlings may enlist the help of beneficial mycorrhizal fungi in their battle to survive and grow above the weed canopy.

What are the most common weeds in deforested sites?

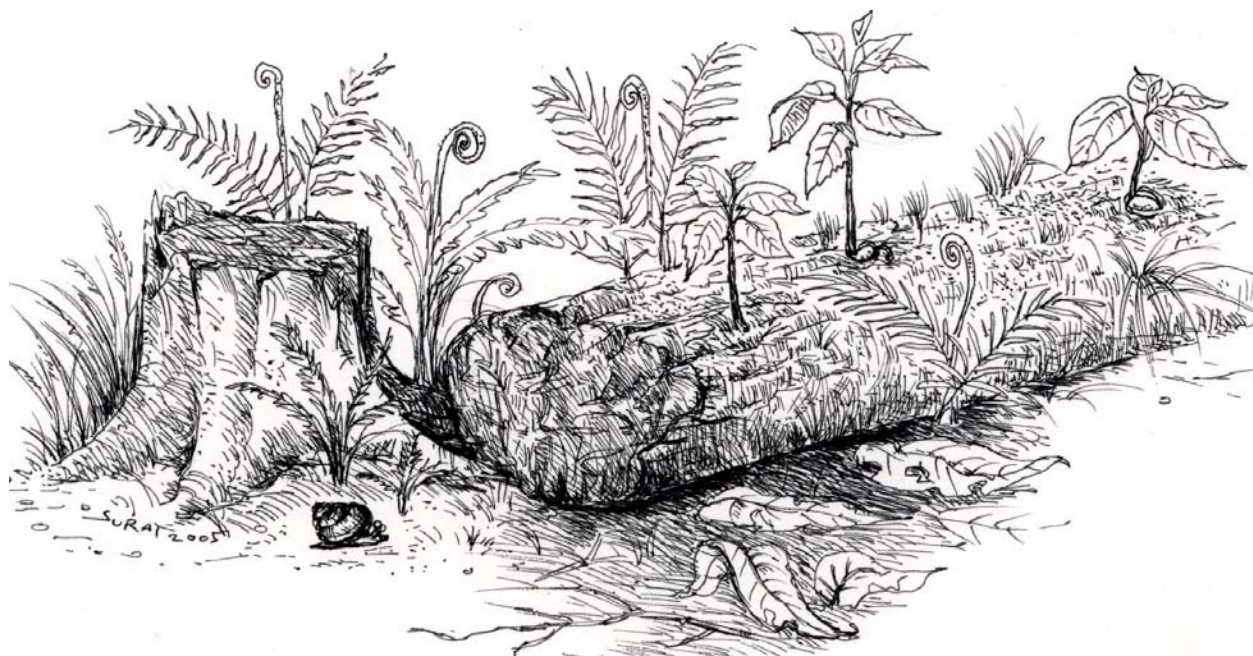
In the mountains of northern Thailand, grasses in tough tussocks, up to 4-5 m tall, often dominate deforested sites (e.g. *Imperata cylindrica*, *Microstegium vagans*, *Panicum notatum*, *Phragmites vallatoria*, *Setaria palmifolia*, *Thysanolaena latifolia* etc. (Gramineae)). Since their growing points are protected from fire by sheaths of toughened leaves, these grasses thrive in fire-prone areas. Looking similar to grasses (but with triangular stems) sedges are also a major component of

the weed communities on deforested sites (e.g. *Cyperus cyperoides*, *Rhynchospora rubra*, *Scleria levis* and so on (Cyperaceae)).

Many weeds are introduced exotic species such as the shrubby-herbs *Eupatorium odoratum* and *E. adenophorum* (Compositae). Species in this family (the daisy family) are particularly successful at colonizing deforested sites. They produce tiny fruits (achenes) either topped with a parachute of fine hairs, for drifting on the breeze, or armed with hooks, which attach to the fur of passing animals (e.g. *Artemisia indica*, *Ageratum conyzoides*, *Bidens pilosa*, *Conyza sumatrensis* and so on). Found all round the world, the hardy bracken fern (*Pteridium aquilinum* (Dennstaedtiaceae)) also dominates vast expanses of treeless hills. It forms a dense canopy, impenetrable to incoming seeds and its dried fronds are a serious fire hazard.

Evergreen vines e.g. *Sbueria involucrata*, *Clitoria mariana*, *Dioscorea* spp etc. and woody climbers e.g. *Millettia pachycarpa* (all Leguminosae, Papilionoideae) can inhibit forest regeneration by smothering tree seedlings, whilst shrubs, such as *Boehmeria chiangmaiensis* (Urticaceae), *Clerodendrum fragrans* (Verbenaceae) and *Triumfetta pilosa* (Tiliaceae) represent more advanced regeneration.

Rotting logs provide excellent germination sites for tree seeds. Relatively free of competition from weeds, the decomposing wood preserves moisture and has excellent structure as a germination medium.



How do weeds prevent forest regeneration?

Light-demanding, herbs rapidly exploit the soil and develop a dense canopy, which absorbs almost all light available for photosynthesis. Amongst such fast-growing plants, small tree seedlings are starved of light, moisture and nutrients. Since trees have evolved to grow tall, they must expend considerable energy and carbon to produce the woody substance, lignin, in order to support their future massive size against gravity. Free of the need to make lignin, herbs can grow much faster than trees. Only when a tree's canopy overtops the weeds and its root system penetrates deeper into the soil than the shallower roots of the weeds does a tree gain an unbeatable advantage over the herbs. Unfortunately, most tree seedlings fade away in the shade of the weeds long before they reach that stage.

Weeds also prevent forest regeneration by providing fuel for fires in the dry season. Most herbaceous weeds survive fire as seeds, corms or tubers, buried in the soil, or they possess well-protected growing points (*e.g.* grasses, cycads, phoenix palms) that resprout after fire. In trees, the growing points are raised on the tips of branches. In a fire, therefore, the small seedlings or saplings of trees are often completely incinerated by the blazing dried weeds surrounding them.

Does weed community structure affect tree establishment?

Some dominant weed species seem to favour forest regeneration more than others. For example, in weed communities dominated by different herb species in Doi Suthep-Pui National Park, Adhikari (1996) found that sites dominated by the shrubby herb, *Eupatorium adenophorum*, supported the highest density and diversity of forest tree seedlings. The tree seedlings established there had higher growth rates and lower mortality rates than in sites dominated by grasses such as *Imperata cylindrica* and *Phragmites vallatoria* or by bracken fern (*Pteridium aquilinum*). Weed communities dominated by bracken seemed particularly resistant to colonization by forest trees.

Could lack of mycorrhizae limit forest regeneration?

Almost all tropical tree species develop symbiotic relationships with fungi that infect their roots to form mycorrhizae (literally "fungus-roots"). Such relationships provide many benefits to host trees and are especially important in enabling seedlings and saplings to out-compete weeds.

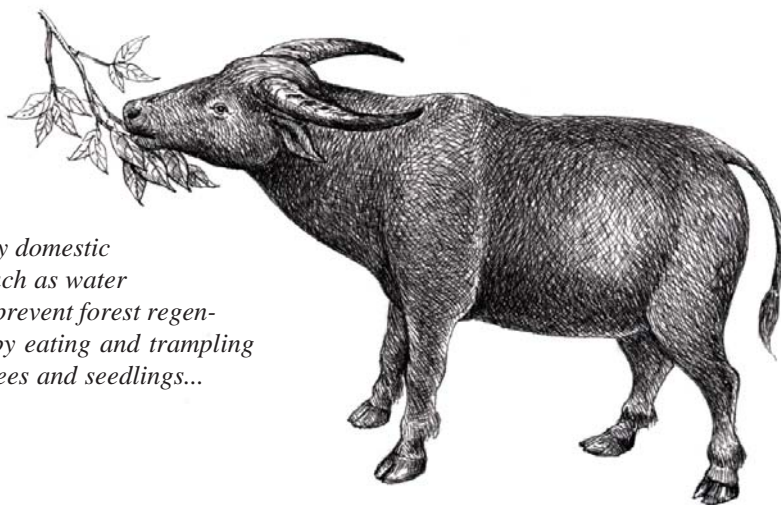
There are two main types of mycorrhizae. Ecto-mycorrhizae (EM) have a sheath of fungal tissue around the tree roots, whereas vesicular-arbuscular mycorrhizae (VAM) lack such a sheath. Almost all tropical tree species form VAM, whereas EM are more restricted to a few unrelated tree families such as the Diptercarpaceae, Fagaceae, Pinaceae and Caesalpinioideae. EM are favoured by seasonally dry conditions.

The most important advantage to trees from mycorrhizae is increased uptake of mineral nutrients, especially phosphorus, which is lacking in tropical soils. Because fungal strands are so much finer than plant roots, they ramify through the soil much more densely, reaching nutrients that thicker tree roots alone cannot reach. Mycorrhizae improve growth and survival of tropical trees. They have also been shown to increase drought resistance, disease resistance and water uptake of their host plants; all benefits that can help trees become established in the harsh conditions of deforested sites.

Could a lack of mycorrhizal fungi inhibit colonization of deforested sites by some tree species? Within dense forest, transmission of most VAM fungi occurs directly between tree roots. Concentrations of fungal spores in the soil are usually very low. For fungus species, which produce above-ground fruiting bodies, spores are dispersed by the wind, but those with under-ground fruiting bodies rely on small rodents and other animals, which eat the spore-laden fruiting bodies and disperse viable spores via their faeces. Therefore, it is very unlikely that even very large deforested areas are completely devoid of all mycorrhizal fungal spores.

However, the question of whether mycorrhizal fungi of the required species are present in sufficiently high densities to infect newly establishing forest tree seedlings warrants further scientific research.





Too many domestic cattle, such as water buffalo, prevent forest regeneration by eating and trampling young trees and seedlings...

Do seedlings have predators?

In most areas, large herbivores like elephants and wild cattle, which could destroy a tree seedling with a single bite, are now so rare that they have no significant impact on forest regeneration at the landscape level. Domestic cattle, on the other hand can be a major impediment to natural forest regeneration.

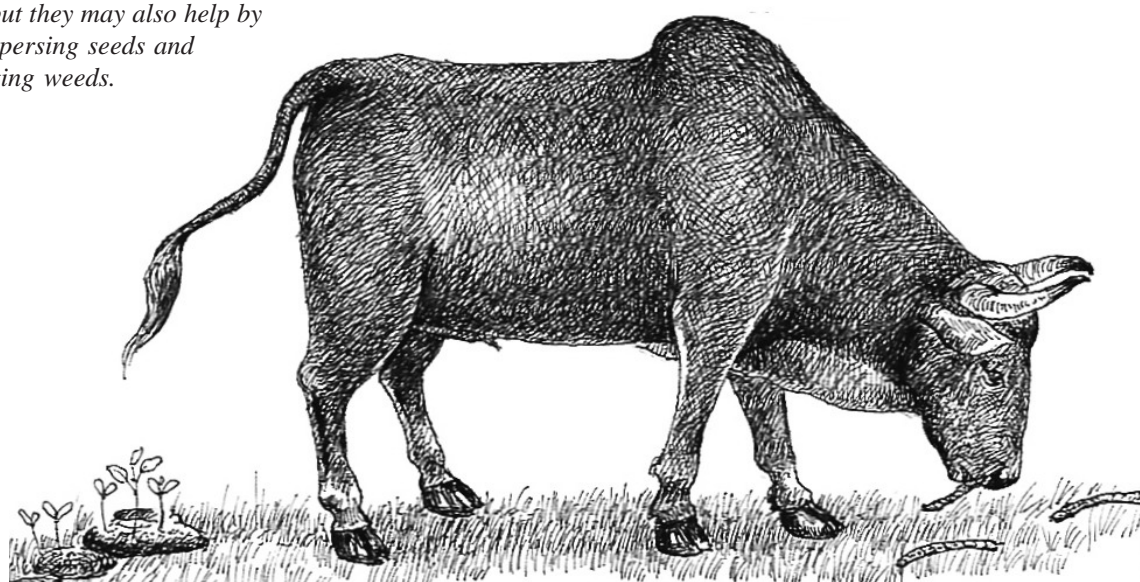
In most tropical countries, it is common to find cows or water buffaloes ranging freely across degraded forestland. The effects of domestic cattle on natural forest regeneration depend on their population density. A small herd might have no significant impact or might even be beneficial in some areas, but where cattle populations are dense, their negative effects usually outweigh any positive effects.

One of the most beneficial effects of cattle can be weed reduction. By grazing on herbaceous weeds, cattle decrease competition for tree seedlings. In addition, domestic cattle can act as seed-dispersers, in the same way as wild cattle can, if they have access to fruits from nearby forest trees. Furthermore, their hoof prints can provide micro-sites for seed germination, where moisture and nutrients accumulate and weeds have been crushed.

The most obvious disadvantage of cattle is that they browse on tree saplings. Cattle can be very selective, often eating the foliage of palatable tree species, whilst ignoring that of unpalatable ones. Distasteful or thorny trees, can thus become dominant, whilst edible ones gradually disappear from the regenerating forest. Cattle also trample young seedlings, indiscriminately and, where large herds follow regular paths, soil compaction can become a problem.

The balance between these positive and negative effects and their relationship with herd density are not fully understood. Furthermore, the effects of cattle on forest regeneration vary greatly with site conditions and vegetation type. Therefore, further research is required to develop models that might be able to predict the overall effects of cattle on forest regeneration at any particular site.

...but they may also help by dispersing seeds and eating weeds.



SECTION 7 – THE ECOLOGY OF FIRE

In the seasonally dry tropics, fires during the hot season are a major constraint to forest regeneration. By the end of the rainy season, weedy vegetation has often grown above head height and is practically impenetrable. In the hot season, this vegetation dies back, dries out and becomes highly flammable. Each time it burns, any tree seedlings that may have managed to gain a root-hold amongst the weeds are usually killed, whereas the weeds survive, re-growing from root stocks or seeds protected beneath the soil. Therefore, the vegetation creates conditions conducive to fire and prevents establishment of trees that could shade out the weeds. Breaking this cycle is the key to restoring seasonally dry tropical forests.

Is fire a natural occurrence in seasonally dry tropical forest?

Fires can be started naturally by lightning strikes, but such natural fires usually occur several years or decades apart. This allows plenty of time for trees to grow large enough to develop some resilience to burning. However, these days, most fires are started by humans. Fires, set to clear fields for cultivation, often spread into surrounding areas, burning young trees and preventing forest regeneration. In many instances, fires are started deliberately to make mushrooms easier to find and to encourage growth of grasses for livestock grazing and to attract wild animals for hunting.

How do fires prevent forest regeneration?

Studies that have compared frequently burnt areas with those protected from fire show that preventing fires accelerates forest regeneration. Meng (1997) and Kafle (1997) compared an area of deciduous dipterocarp-oak forest, protected from fire for 27-28 years with an adjacent frequently burnt area, on the lower slopes of Doi Suthep near Wat Palaht (520 m elevation). They found that frequent fires reduce both the density and species richness of

the tree seedling community, as well as the seed rain (by killing seed-producing trees) and the accumulation of viable seeds in the soil seed bank.

Fire burns off soil organic matter, leading to a reduction in the soil's moisture holding capacity. The drier the soil, the less favourable it is for germination of tree seeds. Burning also reduces soil nutrients. Calcium, potassium and magnesium are lost as fine particles in smoke, whilst nitrogen, phosphorus and sulphur are lost as gases. By destroying the vegetation, fire increases soil erosion by 3-32 times. It also kills beneficial soil micro-organisms, especially mycorrhizal fungi and microbes which break down dead organic matter and recycle nutrients.

Doesn't fire encourage seed germination?

In some ecosystems, fire stimulates seed release and germination, but this effect has not yet been found in the seasonally dry tropical forests of northern Thailand. Hardwick (un-pub.) tested the effects of fire on germination by placing seeds of twelve tree species, from deciduous forest on Doi Suthep, in burning newspaper at a similar temperature to that of a mild litter burn. Seeds of seven of these species were all killed, whilst germination of the others was substantially reduced.

Does fire kill trees?

Most small tree seedlings and sapling are killed by fire, but the larger a tree becomes, the more likely it is to survive. Larger trees have thicker bark, which insulates their vital vascular system (the cambium layer) from the scorching temperatures of forest fires. Stored food reserves in the roots enable larger trees to grow back rapidly, even if their above-ground parts are burned away. The minimum size at which a tree can survive a wild fire varies among species, but as rough rule, a root collar diameter larger than 5 cm usually enables most tree species to survive a moderate burn.



SECTION 8 – THE SURVIVORS

To summarise; it is very difficult for most forest tree species to re-colonize large deforested areas that have become dominated by weeds, mostly because of continued disturbance by humans. Lack of seed sources, disappearance of seed-dispersing animals, competition with hardy, often exotic, weeds and frequent fires all prevent enough tree species establishing at sufficiently high densities to restore the original forest ecosystem. However, a few tree species can overcome these constraints and some of the more common ones, found colonizing large deforested areas in Doi Suthep-Pui National Park, are listed in the table below. Many are deciduous tree species, which grow over a wide range of elevations, and most have small seeds that are easily dispersed by small birds or wind. Where remnant, mature trees of these species still survive in the landscape, there is usually no need to include them in tree planting projects; but wherever they have been eliminated, they are obviously very suitable for planting in degraded areas, especially if mixed with some of the framework tree species described in Part 9.

Table 3.1 – Common tree species observed establishing in open deforested sites at 1,300 m elevation in northern Thailand (FORRU, original data, 2003).

Species	Family	Elevation (m)	Leafing Phenology ¹	Seed Size Class ²	Seed Dispersal ³
<i>Albizia odoratissima</i> (L. f.) Bth.	Leguminosae, Mimosoideae	350-1525	D	M	W
<i>Alstonia scholaris</i> (L.) R. Br. var. <i>scholaris</i>	Apocynaceae	350-1150	D	M	W
<i>Antidesma acidum</i> Retz.	Euphorbiaceae	400-1525	D	M	A
<i>Aporosa dioica</i> (Roxb.) M.-A.	Euphorbiaceae	475-900	D	M	A
<i>Aporosa villosa</i> (Lindl.) Baill.	Euphorbiaceae	500-1500	D	M	A
<i>Aporosa wallichii</i> Hk. f.	Euphorbiaceae	500-1400	D	M	A
<i>Dalbergia cultrata</i> Grah. ex Bth.	Leguminosae, Papilionoideae	350-700	D	L	W
<i>Dalbergia stipulacea</i> Roxb.	Leguminosae, Papilionoideae	500-1400	D	L	W
<i>Debregeasia longifolia</i> (Burm. f.) Wedd.	Urticaceae	525-1685	E	S	A
<i>Dillenia parviflora</i> Griff. var. <i>kerrii</i> (Craib) Hoogl.	Dilleniaceae	375-1000	D	M	A
<i>Engelhardia spicata</i> Lechen. ex Bl.	Juglandaceae	850-1650	D	M	W
<i>Eugenia albiflora</i> Duth. ex Kurz	Myrtaceae	800-1525	E	L	A
<i>Ficus hirta</i> Vahl var. <i>hirta</i>	Moraceae	350-1150	E	S	A
<i>Ficus hispida</i> L. f. var. <i>hispida</i>	Moraceae	350-1525	ED	S	A
<i>Glochidion sphaerogynum</i> (M.-A.) Kurz	Euphorbiaceae	600-1100	D	S	A
<i>Litsea cubeba</i> (Lour.) Pers.	Lauraceae	1100-1685	E	M	A
<i>Markhamia stipulata</i> (Wall.) Seem. ex K. Sch.	Bignoniaceae	950-1550	D	M	W
<i>Myrica esculenta</i> B. -H. ex D. Don	Myricaceae	1300-1500	E	S	A
<i>Phoebe lanceolata</i> (Wall. ex Nees) Nees	Lauraceae	550-1550	E	L	A
<i>Phyllanthus emblica</i> L.	Euphorbiaceae	600-1620	D	M	A
<i>Pterocarpus macrocarpus</i> Kurz	Leguminosae, Papilionoideae	350-900	D	M	W
<i>Schima wallichii</i> (DC.) Korth.	Theaceae	600-1620	E	M	W
<i>Sterculia villosa</i> Roxb	Sterculiaceae	600-1575	D	M	W
<i>Stereospermum colais</i> (B.-H. ex Dillw.) Mabb.	Bignoniaceae	900-1275	D	S	W
<i>Styrax benzoides</i> Craib	Styracaceae	600-1650	E	L	A
<i>Trema orientalis</i> (L.) Bl.	Ulmaceae	1050-1500	ED	M	A

¹E = evergreen; D = deciduous; ED = evergreen/deciduous (trophophilous)

²S= small<0.01 g (dry mass); M= medium 0.01-0.2 g and L= large > 0.2 g

³W= dry fruits mostly dispersed by wind; A= fleshy fruits mostly dispersed by animals, especially small birds

The next obvious question is: how can the many factors that hinder forest regeneration be overcome? We address this crucial issue in Part 4.

